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EFFECTS OF DELAYED REPRODUCTION ON SURVIVAL, FECUNDITY, AND THE RATE OF POPULATION INCREASE

Recently Mertz (1971*a*, 1971*b*) has shown that in decreasing populations deferred reproduction does not necessarily reduce r , the asymptotic rate of population increase (Lotka 1956, chap. 9), even though other life-history

parameters remain unchanged. This result, which contrasts with general expectations from earlier studies (see Cole 1954; Lewontin 1965), was derived for an explicit set of life-history functions. In a recent review of the relationship between delayed reproduction in males and polygynous mating systems (Wiley 1974), I examined possible effects of delayed breeding in populations with $r = 0$. To examine the relationship between the effects of delayed reproduction and the rate of population increase, I present here a more general formulation of the problem.

It will become clear that, for *any* initial value of r , delayed reproduction will increase, decrease, or have no effect on r , depending on the effects of delayed reproduction on particular life-history parameters. More important, the results specify the interacting contributions of early survival and later fecundity, as a result of delayed reproduction, in maintaining a given rate of population increase (see Lewontin 1965; Williams 1966; Gadgil and Bossert 1970).

My approach is to use Lotka's (1956, chap. 9) equation in comparing hypothetical populations with identical rates of increase but different age-specific survival and age-specific fecundity. This approach can identify the changes in one of these life-history functions necessary to compensate changes in the other, such that r remains constant. In using Lotka's equation to examine life-history functions in relation to per-capita rates of population increase, one must remember that this equation requires a stable age distribution and stable age-specific survival rates and fecundity. For populations with stationary mean size, including those regulated by constant density-dependent influences, the equation with $r = 0$ would thus apply best to long-term averages for age-specific survival and fecundity. Lotka's equation, although strictly pertinent only to populations (Hairston et al. 1970), can also provide a basis for understanding at least the initial fitnesses of genes that affect life-history functions and thus for understanding the evolution of life-history strategies (Fisher 1958, chap. 2; Charlesworth 1973). Charlesworth (1973) has demonstrated that the spread of a rare, incompletely recessive gene is favored if it initially affects the age-specific survival and fecundity of heterozygotes, so that the value of r for a hypothetical population of heterozygotes is greater than that for a population of the common homozygote. Because persistence of a gene in a population depends strongly on its tendency to increase in frequency when its frequency is near zero, effects of a mutant gene on the life-history functions of heterozygotes are then critical for the gene's persistence in a population.

The present formulation includes parameters pertinent to the life histories of many vertebrates with discrete annual breeding seasons. I assume a life history divided into three periods with different survival rates: juvenile, during the first year; adolescent, prior to the onset of breeding; and adult, after the onset of breeding. Take annual survival for adults equal to s , annual survival for adolescents equal to A_s , and that for juveniles equal to J_s ($0 < s, A_s, J_s < 1$). Then, employing Lotka's equation in its discrete form,

$$\sum_{x=0}^{\infty} \lambda^{-x} J A^{(a-1)} s^x m(x) = 1,$$

where $\lambda = e^r = N(t+1)/N(t)$ with t in units of years, $m(x)$ is age-specific fecundity, and a (≥ 1) is the age at onset of reproduction.

Now, if the onset of reproduction is postponed d years, such that age-specific fecundity is displaced d years and multiplied by a factor M , then for this second strategy $m'(x+d) = Mm(x)$. If this strategy also increases juvenile and adolescent survival by a factor E , where $1 \leq E < 1/As$, then

$$1 = \sum_{x=0}^{\infty} \lambda'^{-(x+d)} E^{(x+d)} J A^{(a-1+d)} s^{(x+d)} M m(x) = (\lambda'^{-1} A s)^d M E^{(a+d)} \left[\sum_{x=0}^{\infty} \lambda'^{-x} J A^{(a-1)} s^x m(x) \right].$$

If this postponement of breeding neither increases nor decreases λ , so $\lambda = \lambda' = \lambda_{nd}$, the λ of no difference, then

$$M E^{(a+d)} (A s \lambda_{nd}^{-1})^d = 1$$

and

$$A s (M E^{a+d})^{1/d} = \lambda_{nd}.$$

This equation then relates parameters of survival and fecundity to λ , such that λ does not change with delayed breeding. More generally $\lambda' \begin{matrix} \geq \\ \leq \end{matrix} \lambda$ when $A s (M E^{a+d})^{1/d} \begin{matrix} \geq \\ \leq \end{matrix} \lambda'$. Thus $\lambda < \lambda' < \lambda_{nd}$ or the converse. To compensate for a delay of d years in the onset of breeding, the proportionate change in the expected production of offspring, $(M E^{a+d})^{1/d}$, must equal λ/As .

When deferred reproduction increases fecundity at the start of breeding ($M > 1$), delayed reproduction is more likely to increase λ (Williams 1966), for λ_{nd} increases with $M^{1/d}$. Note that when $M = 1$, which includes the case of constant annual fecundity regardless of delayed breeding [$m(x) = m(x+d) = c$], and $E = 1$, then λ_{nd} equals the adolescent survival rate (As): just as we should expect, in the absence of any other changes in life history, delayed breeding results in increased λ only when annual prebreeding survival exceeds the proportionate annual change in population size.

When $E = 1$ in the present formulation, deferred reproduction results in an extension of adolescent survival rates (As) to later ages but not in an increase in early survival rates. Under these conditions, unless fecundity increases concurrently, deferred reproduction will decrease in all stable or increasing populations. Because $As < 1$, then $\lambda_{nd} < 1$, when $E = 1$ and $M \leq 1$.

The situation changes if deferred reproduction increases prebreeding survival ($E > 1$). To isolate effects of early survival on the consequences

of delayed reproduction, let $M = 1$. Then, even though $As < 1$, λ_{nd} could exceed 1, depending on values of E , a , and d . Deferred reproduction could increase λ in stable or some increasing populations provided that deferred breeding coincided with a sufficient increase in early survival.

Note that an increase in survival only between ages a and $a + d$, as a result of delayed breeding, results in $\lambda_{nd} = AsEM^{1/d}$. Because $EAs < 1$, in these circumstances $\lambda_{nd} < 1$, when $M \leq 1$. Thus when the only effect of delayed reproduction is an increase in survival between ages a and $a + d$, delayed reproduction would decrease λ in stable or increasing populations.

The way in which organisms allocate their available time and nutrients to survival, growth, and reproduction at different ages in part determines their life-history functions. As both depend on an individual's allocation of its resources, these functions are not independent. The possibility that deferred reproduction might actually increase early survival thus seems plausible whenever reproduction entails considerable investment of time and nutrients or exposure to predators. In addition, if deferred breeding could enhance the development of foraging skills by young individuals, then deferred breeding might increase their parental skills at later ages, which in turn could increase the early survival of their offspring, so that $E > 1$. Increased early growth as a result of postponed reproduction might increase early survival and, in addition, later parental capabilities or fecundity. The question posed for studies of particular populations is whether the allocation of additional time and nutrients for survival has effects on age-specific survival sufficient to compensate for the effects that the withdrawal of these resources from reproduction have on age-specific fecundity.

To summarize, in stable populations ($\lambda = 1$) deferred onset of reproduction will tend to increase λ ($\lambda_{nd} > 1$) provided deferred breeding coincides with a sufficient increase in later fecundity (M) or a sufficient increase in early survival (E), such that $ME^{(a+d)} > (As)^{-d}$. No ratio of adolescent to adult survival (A) will alone result in increased λ as a result of deferred reproduction in any stable or increasing population or in those decreasing populations where initial $\lambda > As$. An increase in survival only between ages a and $a + d$ will not result in increased λ with delayed breeding in populations with initial $\lambda > EAs$.

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